

Title: Tree height and hydraulic traits shape growth responses across droughts in a temperate broadleaf forest

Authors: Ian R. McGregor^{1,2}, Ryan Helcoski¹, Norbert Kunert^{1,3}, Alan J. Tepley^{1,4}, Erika B. Gonzalez-Akre¹, Valentine Herrmann¹, Joseph Zailaa^{1,5}, Atticus Stovall^{1,6,7}, Norman A. Bourg¹, William J. McShea¹, Neil Pederson⁸, Lawren Sack^{9,10}, Kristina J. Anderson-Teixeira^{1,3*}

Author Affiliations:

1. Conservation Ecology Center; Smithsonian Conservation Biology Institute; National Zoological Park, Front Royal, VA 22630, USA
2. Center for Geospatial Analytics; North Carolina State University; Raleigh, NC 27607, USA
3. Center for Tropical Forest Science-Forest Global Earth Observatory; Smithsonian Tropical Research Institute; Panama, Republic of Panama
4. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada
5. Biological Sciences Department; California State University; Los Angeles, CA 90032, USA
6. Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, USA
7. NASA Goddard Space Flight Center; Greenbelt, MD 20771, USA
8. Harvard Forest, Petersham, MA 01366, USA
9. Department of Ecology and Evolutionary Biology; University of California, Los Angeles; Los Angeles, CA 90095, USA
10. Institute of the Environment and Sustainability; University of California, Los Angeles; Los Angeles, CA 90095, USA

*corresponding author: teixeirak@si.edu; +1 540 635 6546

Text	word count	other	n
Total word count (excluding summary, references and legends)	currently ~6442 (strict limit 6,500)	No. of figures	2 (both colour)
Summary	currently 200 (limit 200)	No. of Tables	5
Introduction	currently ~1339	No of Supporting Information files	6
Materials and Methods	currently ~1604		
Results	currently ~1558		
Discussion	currently ~1866 (limit 30% of total (not strict), or 1950 if manuscript reaches word limit)		
Acknowledgements	currently ~73		

Summary

- As climate change is driving increased drought in many forested regions around the world, mechanistic understanding of factors conferring drought resistance in trees is increasingly important. The dendrochronological record provides a window through which we can understand how tree size and species' traits interactively shape tree growth responses during droughts.
- We analyzed tree-ring records for twelve species of an oak-hickory forest - representing 97% of woody productivity - in the 25.6-ha ForestGEO plot in Virginia (USA) to determine how tree size, microenvironment characteristics, and species' traits interactively shape drought responses across the three strongest regional droughts over a 60-year period (1950 - 2009).
- Individual-level drought resistance decreased with tree height, which was the dominant size-related variable affecting drought response. Resistance was greater among species whose leaves lost turgor (wilted) at more negative water potentials, and whose leaves experienced less shrinkage upon dessication. However, there was substantial variation in the best predictor variables across the three drought periods.
- We conclude that hydraulic traits and tree height influence growth responses during drought, and can explain variation in the tree ring record spanning historical droughts. Thus, these traits can be useful for predicting future drought responses under climate change.

Key words: annual growth; canopy position; drought; Forest Global Earth Observatory (ForestGEO); leaf hydraulic traits; temperate broadleaf deciduous forest; tree height; tree-ring [5-8] *Five to eight key words (in alphabetical order) . Words that are in the title can, and should, be among these.*

Introduction

See comment 4,31

Forests globally play a critical role in climate regulation (Bonan, 2008), yet there remains enormous uncertainty as to how the terrestrial carbon (C) sink, which is dominated by forests, will respond to climate change (Friedlingstein et al., 2006). An important aspect of this uncertainty lies with physiological responses of trees to drought (Kennedy et al., 2019). In many forested regions around the world, the risk of severe drought is increasing (Trenberth et al., 2014; Cook et al., 2014, 2015; Mankin et al., 2019) Dai et al. 2018 **{too many}**, often despite increasing precipitation (Intergovernmental Panel on Climate Change, 2015). Droughts, exasperated by climate change, have been affecting forests worldwide (Allen et al., 2010), and are expected to continue severely impacting forests (Anderegg et al., 2013; Adams et al., 2009; Bréda et al., 2006; Hartmann et al., 2018; Allen et al., 2015; Abrams and Nowacki, 2016; Adams et al., 2017) **{too many refs here. reduce to 2-3}**. However, it is difficult to resolve factors conferring drought resistance in trees with the limited available census data, which only rarely includes extreme drought. The aim of this study was to test how tree size and traits shaped growth responses to historical droughts in the tree-ring record.

One fundamental question regarding forest responses to drought is what drives the observed tendency for large trees to suffer more during drought. Bennett et al. (2015) was the first to show greater growth reductions for larger trees on a global scale, and numerous subsequent studies have reinforced this finding (*e.g.*, Stovall et al. (2019); Hacket-Pain et al. (2016)). However, it has yet to be resolved which of several potential underlying mechanisms drive this pattern. First, taller trees have a greater biophysical challenge of lifting water greater distances against the effects of gravity and friction (McDowell et al., 2011; McDowell and Allen, 2015; Ryan et al., 2006; Couvreur et al., 2018), especially during drought (Zhang et al., 2009). Second, larger trees may have lower drought resistance because of their higher crown positions, where they are exposed to higher solar radiation, greater wind speeds, and lower humidity [Koike et al. (2001); Kunert et al. (2017) **REFS-KAT**]. Subcanopy trees subsequently tend to fare better specifically due to the benefits of a buffered environment (Pretzsch et al., 2018). Potentially counteracting the biophysical challenges faced by large trees, their larger root systems confer a potential advantage in terms of allowing greater access to water; however, it appears that this effect is usually insufficient to offset the costs of height and/or crown exposure. *A final mechanism that could mediate tree size-related responses to drought is how hydraulic traits are distributed with respect to size (Meakem et al., 2018; Liu et al., 2019, Roskill et al. 2019).*

{LS:—larger trees may have larger xylem conduits, which in turn may have less resistance to air seeding and subsequent embolism (Mark Olsen argument, right?) } *The pattern observed by Bennett et al. (2015) could be caused if the larger size classes were dominated by species less adapted to handle drought. Alternatively, larger size classes may be dominated by species that are inherently better adapted to greater biophysical challenges—as is the case in tropical moist forests of Panama, where larger size classes contain greater proportions of deciduous species (Condit et al., 2000; Meakem et al., 2018). Understanding the mechanisms driving the greater growth reductions of larger trees during drought will require sorting out the interactive effects of height, canopy position, soil water availability, and species’ traits. {see Lawren’s comment on order of presentation}*

Debates have also arisen regarding the traits that would influence tree growth responses to drought. Commonly-measured traits including wood density (*WD*) and leaf mass per area (*LMA*) have been linked to drought responses in some temperate deciduous forests (Abrams, 1990; Guerfel et al., 2009; Hoffmann et al., 2011) and other forest biomes around the world (Greenwood et al., 2017). However, in other cases these

traits have failed to explain drought responses (**REFS**), and the direction of response is not always consistent; for instance, higher *WD* has been associated with greater drought resistance at a global scale (Greenwood et al., 2017) but correlated negatively with tree performance during drought in a broadleaf deciduous forest in the southeastern United States (Hoffmann et al., 2011). Thus, their role may be due to indirect correlations with other traits within life-history strategies (Hoffmann et al., 2011). Recent work has shown a great potential for hydraulic traits to predict growth and mortality responses. Hydraulic traits including water potentials at which percent loss conductivity surpass a certain threshold (*P*50, *P*80, *P*88) and hydraulic safety margin have enabled prediction of drought performance (Anderegg et al., 2018) but are time-consuming to measure and therefore infeasible for predicting or modeling drought responses in highly diverse forests (*e.g.*, in the tropics). More rapidly measurable leaf hydraulic traits with direct linkage to plant hydraulic function are emerging with potential to explain greater variation in plant distribution and function than the more commonly-measured *WD* and *LMA* (Medeiros et al., 2019). These include leaf area shrinkage upon desiccation (*PLA_{dry}*; (Scoffoni et al., 2014)) and the leaf water potential at turgor loss point (π_{tlp}), *i.e.*, the water potential at which leaf wilting occurs (Bartlett et al., 2016). The abilities of both *PLA_{dry}* and π_{tlp} to explain tree performance under drought remains untested.

KAT is here with integrating LS comments

A final central question regarding forest responses to drought is whether tree size and species' traits have similar influence across different drought events, or whether that influence is more strongly predicted by community-level responses to variable drought severity, duration, and timing based on tree size and traits. Tree growth responses vary with drought characteristics such as timing and atmospheric demand (D'Orangeville et al., 2018), but the question of how tree size and species' traits impact growth responses across droughts still remains. While tree-ring studies provide long-term records of tree responses to multiple droughts (*e.g.*, (Lloret et al., 2011; D'Orangeville et al., 2018) **REFS**), they generally focus on species-level responses, and do not consider the roles of tree size and microenvironment. The ecological field-based studies that have shaped our understanding of the role of tree size and microenvironment in forest drought responses generally examine only a single drought and tend to focus disproportionately on extreme droughts with dramatic impacts (*e.g.*, [Allen et al. (2010); Bennett et al. (2015); Stovall et al. (2019); Anderegg et al. (2016)]). Thus, our knowledge of forest responses to more modest but frequent droughts - *e.g.*, those with historical return intervals on the order of one to two decades - remains limited. There is evidence that the degree to which larger trees are more impacted by drought increases with the severity of drought conditions (Bennett et al., 2015; Stovall et al., 2019), so the influence of tree size may be less in weaker—but more common—droughts. Thus, while we expect many of the mechanisms shaping drought responses to be universal, we have little understanding of how tree size and traits interact with drought characteristics.

To yield functional understanding of how tree size, microenvironment characteristics, and species' traits collectively shape drought responses, we test a series of hypotheses and associated specific predictions (Table 1) based on the combination of tree-ring records from three droughts (1966, 1977, 1999), species functional and hydraulic trait measurements, and forest census data from a 25.6-ha ForestGEO plot in Virginia (USA). First, we focus on the role of tree size and its interaction with microenvironment. We confirm that, consistent with most forests globally, larger-diameter trees tend to have lower drought resistance in this forest, which is in a region (eastern North America) represented by only two studies in (Bennett et al., 2015) (*H1.0*). We then test hypotheses designed to disentangle the relative importance of tree height (*H1.1*), crown exposure (*H1.2*), and soil water availability, which should be greater for larger trees in dry but not in

perpetually wet microsites (*H1.3*). Second, we focus on the role of species’ functional and hydraulic traits and their interaction with tree height. We test predictions that drought resistance is **negatively** correlated with wood density (following patterns observed by Hoffmann et al. (2011)) and positively correlated with specific leaf area, but that hydraulic leaf traits including PLA_{dry} and π_{tlp} are better predictors (*H2.1*). We expect that ring-porous species would have greater drought resistance than semi-ring and diffuse-porous species, as has been previously observed (Kannenberget al., 2019; Elliott et al., 2015; Friedrichs et al., 2009). We then test whether these traits correlate with tree height (*H2.2*), potentially driving the observed tendency for taller trees to suffer more during drought after accounting for trait effects (*H2.3*). Finally, we focused on variability among droughts, asking how community resistance varied across droughts (*H3.1*) and whether the factors confirming vulnerability or resistance varied across droughts (*H3.2*).

Materials and Methods

Study site

Research was conducted at the 25.6 ha ForestGEO (Forest Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53’36.6”N, 78°08’43.4”W) (Bourg et al., 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains at the northern edge of Shenandoah National Park. Elevations range from 273-338m above sea level with a topographic relief of 65m (Bourg et al., 2013). Climate is humid temperate, with mean annual temperature of 12.7°C and precipitation of 1005 mm during our study period (1960-2009; source: CRU TS v.4.01; Harris et al. (2014)). Dominant tree taxa within this secondary forest include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.).

Data collection and preparation

All analysis beyond basic data collection was performed using R version 3.5.3 (R Core Team, 2019).

Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree size, microenvironment characteristics, and species traits (Table 2). The SCBI ForestGEO plot was censused in 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems ≥ 1 cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit, 1998). From this census data, we used measurements of DBH from 2008 to calculate historical DBH and data for all stems ≥ 10 cm to analyze functional trait composition relative to tree height (all analyses described below). Census data, which were last updated in 2019, are available through the ForestGEO data portal (www.forestgeo.si.edu).

We analyzed tree-ring data (cambial growth increment) from 571 trees representing the twelve species contributing most to woody aboveground net primary productivity ($ANPP_{stem}$), which together comprised 97% of study plot $ANPP_{stem}$ between 2008 and 2013 (Helcoski et al., 2019) (Figure S1). Cores were collected within the ForestGEO plot at breast height (1.3m) in 2010-2011 or 2016-2017 using a 5mm increment borer. In 2010-2011, cores were collected from randomly selected live trees of species with at least 30 individuals ≥ 10 cm DBH (Bourg et al., 2013). In 2016-2017, cores were collected from all trees found dead in the annual mortality census (Gonzalez-Akre et al., 2016). Cores were sanded, measured, and cross-dated using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies have been published in association with Helcoski et al. (2019): (ITRDB; GitHub/Zenodo). **Ryan, have you heard back from ITRDB? We should also cite GitHub/Zenodo here.**

For each cored tree, we combined tree-ring records and allometric equations of bark thickness to retroactively calculate DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

$$DBH_Y = DBH_{2008} - 2 * \left[\sum_{year=Y}^{2008} (r_{ring,Y} : r_{ring,2008}) - r_{bark,Y} + r_{bark,2008} \right]$$

Here, Y denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark thickness. Bark thickness was estimated from species-specific allometries based on the bark thickness data from the site (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression equations on log-transformed data to relate bark thickness to diameter inside bark from 2008 data (Table S1), which were then used to determine bark thickness in the retroactive calculation of DBH.

Height measurements (H , $n=1518$ trees) were taken by several researchers between 2012 to 2019, and are archived in a public GitHub repository. Measurement methods included manual (Stovall et al., 2018a; NEON, 2018), digital rangefinders (Anderson-Teixeira et al., 2015b; NEON, 2018), and automatic, ground-based LiDAR (Stovall et al., 2018b). Rangefinders used either the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. Both methods are associated with some error (Larjavaara and Muller-Landau, 2013), but in this instance there was no clear advantage of one or the other. Measurements from the National Ecological Observatory Network (NEON) were collected nearby the ForestGEO plot following standard NEON protocol, whereby vegetation of short stature was measured with a collapsible measurement rod, and taller trees with a rangefinder (NEON, 2018). Species-specific height allometries were developed (Table S2) using logarithmic regression ($\ln[H]$). For species with insufficient height data to create reliable species-specific allometries, heights were calculated from an equation developed using all height measurements.

Crown positions (CP) were recorded for all cored trees that remained standing during the growing season of 2018. We followed the crown position protocol of Jennings et al. (1999), whereby positions were ranked as dominant, codominant, intermediate, or suppressed. While some trees undoubtedly changed position in the 52 years between the 1966 drought and our observations in 2018, in this case the bias would be unlikely to result in false acceptance of our hypothesis (i.e., type I error unlikely; type II error possible). An analysis of crown position relative to height (Fig. 2d) and height changes since the beginning of the study period indicated that changes were fairly small relative to differences among canopy positions, although dominant and co-dominant trees were similar in height (Fig. S3). Specifically, average tree height growth was confined to ~ 0.82 m from 1966 to 1977, ~ 1.45 m from 1977 to 1999, and ~ 1.97 m from 1999 to 2018.

While some canopy positions undoubtedly shifted in the $\#$ years between the 1966 drought and our observations in 2018, change was relatively slow, and bias would more likely result in type x error with regards to testing our hypothesis.

Topographic wetness index (TWI) was calculated using the dynatopmodel package in R (Figure S1) (?). Originally developed by Beven and Kirkby (1979), TWI was part of a hydrological run-off model and has since been used for a number of purposes in hydrology and ecology (Sørensen et al., 2006). TWI calculation depends on an input of a digital elevation model (DEM), and from this yields a quantitative assessment defined by how “wet” an area is, based on areas where run-off is more likely. From our observations in the plot, the calculation of TWI performed comparatively better at categorizing wet areas than the calculation of

a distance matrix from a stream shapefile.

Hydraulic traits were collected at SCBI (Table 3) in August 2018. We sampled small sun-exposed branches within eight meters of the ground from three individuals of each species in and around the ForestGEO plot. Sampled branches were re-cut under water at least two nodes above the original cut and re-hydrated overnight in covered buckets (opaque plastic bags) before measurements were taken. Rehydrated leaves taken towards the apical end of the branch ($n=3$ per individual: small, medium, and large) were scanned, weighed, dried at 60°C for ≥ 48 hours, and then re-scanned and weighed. Leaf area was calculated from scanned images using the LeafArea R package (?). *LMA* was calculated as the ratio of leaf dry mass to fresh area. *PLA* was calculated as the percent loss of area between fresh and dry leaves. *WD* was calculated for $\sim 1\text{cm}$ diameter stem samples (bark and pith removed) as the ratio of dry weight to volume, which was estimated using Archimedes' displacement. We used the rapid determination method of Bartlett et al. (2012) to estimate water potential at turgor loss point (π_{tlp}). Briefly, two 4mm diameter leaf discs were cut from each leaf, tightly wrapped in foil, submerged in liquid nitrogen, perforated 10-15 times with a dissection needle, and then measured using a vapour pressure osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential (π_{osm}) given by the osmometer was used to estimate (π_{tlp}) using the equation $\pi_{tlp} = 0.832\pi_{osm}^{-0.631}$ (Bartlett et al., 2012). Data for hydraulic traits are available at [**create new public GitHub repo for hydraulic traits, archive in Zenodo, give DOI**].

To characterize how environmental conditions vary with height, data were obtained from the National Ecological Observation Network (NEON) tower located $<1\text{km}$ from the study area. We used data on wind speed, relative humidity, and air temperature, all measured over a vertical profile spanning from 7.2 m height to above the top of the tree canopy (31.0 or 51.8m, depending on censor), for the years 2016-2018 (?). After filtering for missing and outlier values, the data were consolidated to represent the mean values per sensor height per day. The range of these means were then aggregated at a month scale.

Identification of drought years

We identified droughts within the time period 1950-2009, defining drought (Slette et al., 2019) as events with widespread reductions in tree growth and anomalously dry peak growing season climatic conditions. Simultaneous consideration of both meteorological conditions and tree growth ensured that drought was the primary driver of observed growth declines and that our focus remained on droughts that substantially impacted the forest community. Candidate drought years were defined as those where $>25\%$ of the cored trees experienced $>30\%$ reduction in basal area increment (BAI) relative to the previous 5 years, following the drought resistance (*Rt*) metric of (Lloret et al., 2011), and identified using the pointRes package (?) in R. Specifically, *Rt* values ≤ 0.7 indicated growth reductions, whereas values ≥ 1.0 indicated increased growth. Separately, we identified the years with driest conditions during May-August, which stood out in the analysis of (Helcoski et al., 2019) as the current-year months to which annual growth was most sensitive for trees at this site. We considered two metrics of moisture deficit: NOAA Divisional Data's Palmer Drought Severity Index (PDSI) and the difference between monthly potential evapotranspiration (PET) and precipitation (PRE). These data were obtained from the ForestGEO Climate Data Portal (<https://github.com/forestgeo/Climate>) in August 2018, with monthly PET and PRE sourced from Climatic Research Unit high-resolution gridded dataset (CRU TS v.4.01; Harris et al. (2014)). The driest years were identified through ranking mean May-August PDSI or [PET-PRE] for the time period from driest to wettest.

Statistical Analysis

For each drought period, we calculated drought resistance (R_t) as the ratio of BAI during drought to the mean BAI over the five years preceding the drought (Lloret et al., 2011). Thus, $R_t < 1$ indicates reduced growth under drought. Analyses focused on testing the predictions presented in Table 1, with either R_t or H as the response variable. The general statistical model for hypothesis testing was a mixed effects model (lme4 package from ?) with R_t as the response variable, tree nested within species as a random effect, and one or more independent variables as fixed effects. We used AICc (AICcmodavg package from ?) to assess model selection, and conditional/marginal R-squared to assess model fit.

Models were run for all drought years combined (with year as a fixed effect) and for each drought year independently. In order to determine the relative importance of the traits alone (H2.1), we first tested the predictor variables independently against both height and R_t given height's substantial influence. Variables were considered useful for predicting R_t when AICc was reduced by ≥ 2 relative to the appropriate null model lacking that variable (Table 4).

Once these beset predictor variables were determined, we calculated the best overall models for predicting R_t across all traits, each individual drought year, and all years combined. We compared models with all possible combinations of candidate variables and identified the full set of models within $\Delta AICc = 2$ of the top model (that with lowest AICc). These were counted as the “top multivariate models”. When a variable appeared in all of these top models and the sign of the coefficient was consistent across models, this was counted as support for/ rejection of the associated prediction by the multivariate models. If the variable appeared in only some of the models, we considered this partial support. **see comment 27**

Results

Focal droughts and their characteristics

Nobby questions using “useful predictor” as a term, instead using more jargon I think In the 60-year period between 1950 and 2009, there were three droughts that met our criteria of anomalously dry climatic conditions coupled with substantial reductions in tree growth: 1966, 1977, and 1999 (Figs. 1, S2). We excluded one year (1991) meeting the growth reduction criteria (26.5% of trees experienced $>30\%$ growth reduction, mean resistance = -13.8%) because this year was not among the driest in terms of May-August [PET-PRE] or PDSI (Table S3). Rather, the severity of growth reduction may be explained in part by defoliation from gypsy moths (*Lymantria dispar* L.) from approximately 1988-1995, which strongly impacted *Quercus* spp. (Cite Shenandoah paper, if accepted; Twery, 1991).

Climatically, these drought years included three of the five years between 1950 and 2009 with greatest moisture deficit (PET-PRE) during the peak growing season months of May-August (MJJA), which for this site are when annual tree growth is most sensitive (Helcoski et al., 2019). Specifically, 1966, 1977, and 1999 had mean MJJA PET-PRE of 83, 87, and 80 mm mo⁻¹, respectively. The years 1964 and 2007 also ranked in the top five driest (PET-PRE = 84 and 82 mm mo⁻¹), but were not among the lowest in terms of PDSI and were thus not identified as candidate years for inclusion as top drought years (Table S3).

The droughts differed in intensity and prior onset (Table S3, Fig. S2). 1999 for example was the most intense (having the lowest PDSI) during May-July, while 1966 had a more intense August PDSI and overall had the second strongest drought during the growing season. The 1977 drought was the least intense throughout the growing season. All droughts increased in intensity from May through August, but differed in the previous months. The 1966 drought was preceded by two years of moderate drought during the growing season and

severe to extreme drought starting the previous fall. Similarly, the 1999 drought was preceded by severe to extreme drought starting the previous fall, but before that conditions were wetter than average until the previous June. The 1977 drought was preceded by 2.5 years of near-normal conditions, and was therefore the mildest of the three droughts by any measure.

Community-level tree growth responses to these droughts were modest, with mean resistance values of 0.86, 0.84, and 0.86 for 1966, 1977, and 1999, respectively (Fig. 1b). All droughts yielded about 5% more trees experiencing negative growth ($Rt \leq 0.7$) as defined by our drought threshold, specifically, 29% in 1966, 32% in 1977, and 27% in 1999. However, some trees exhibited increased growth: ($Rt > 1.0$): 26% in 1966, 22% in 1977, and 26% in 1999.

Tree size and drought resistance

Overall, our analysis confirmed the tendency for larger-diameter trees to show greater reductions in growth during drought (Bennett et al., 2015) (*H1.0*), although there was no significant effect during 1977 or 1999 individually (Tables 1, 4). The same held true for $\ln[H]$ as a univariate predictor (*H1.1*; Tables 1, 4). When combined with other predictor variables in our multivariate models, the top models usually included an effect of $\ln[H]$, and its coefficient was consistently negative, as predicted (Tables 1, 5). We note that a non-significant positive correlation between $\ln[H]$ and Rt for 1999 became negative in the context of the multivariate models, again supporting *H1.1* (Table 1).

Crown position was generally correlated with H , but with substantial variation (Fig. 2d). Crown position was a much poorer predictor of Rt than was H (Table 4), lending little overall support to *H1.2* (Table 1). When considered alone, CP had a significant response only in the 1966 drought, during which trees with dominant CP had the lowest Rt . When considered in conjunction with H , CP resulted as a significant predictor only for the 1999 drought, during which suppressed and then intermediate trees had the lowest Rt . Crown position was included in almost half of the top models, with mixed results as to how Rt varied with CP (Table 5). Most commonly in these multivariate models, as in the univariate models (Table 4), the resistance of dominant trees was less than that of co-dominant trees but higher than that of suppressed trees. Although CP was a useful predictor of Rt , it overall had a weak effect relative to that of H .

In the non-drought years for which we have vertical profiles in climate data (2016-2018), taller trees—or those in dominant crown positions—were generally exposed to higher evaporative demand during the peak growing season months (May-August; Fig. 2). Specifically, maximum daily wind speeds were significantly higher above the top of the canopy (40-50m) than within and below (10-30m) (Fig. 2a). Relative humidity was also somewhat lower during June-August, ranging from ~50-80 above the canopy and ~60-90% in the understory (Fig. 2b). Air temperature did not vary across the vertical profile (Fig. 2c).

Resistance was negatively correlated with $\ln[TWI]$ (Tables 4-5), negating the hypothesis that trees in moist microsites would suffer less during drought. Nevertheless, we tested for a negative $\ln[H] * \ln[TWI]$ interaction (*H1.3*), which could indicate that smaller trees (with smaller rooting volume) are more susceptible to drought in drier microenvironments that have a deeper water table. *H1.3* was rejected; the $\ln[H] * \ln[TWI]$ interaction was never significant and had a consistently positive coefficient (Table 4).

Species' traits, height, and drought resistance

Our results partially support Hypothesis *H2.1*, where species' hydraulic traits — XP , PLA_{dry} , and π_{tlp} —were sometimes useful in explaining variation in drought responses, whereas LMA and WD never significantly

associated with Rt in the univariate models (all $dAIC \leq 0.22$; Tables 1,4,5). Therefore, these were excluded as candidate variables for the full multivariate models. In contrast, XP , PLA_{dry} , and π_{tlp} all explained modest amounts of variation ($dAIC > 1.0$) in at least one drought (Table 4). PLA_{dry} was a strong predictor for the 1966 drought and all droughts combined, with consistently negative coefficients. π_{tlp} was not significant in the univariate models but had a consistently negative coefficient (Table 4). Whereas ring-porous species had highest Rt overall and in the 1966 and 1999 droughts, they had lower Rt in 1977. Results were similar in the context of multivariate models (Table 5), except that PLA_{dry} had a small positive coefficient in the one 1999 model in which it was included. PLA_{dry} , and π_{tlp} were each included in the top overall model and in the top model for two of the three individual droughts (Table 5).

The results reject Hypothesis $H2.2$, finding no evidence that taller trees had traits associated with greater drought resistance. In part because of the large sample size ($n=7549$ trees—all individuals of our 12 focal species ≥ 10 cm in 25.6 ha), there were significant ($p<0.0001$) correlations of H with all species' traits (see Table S4). **see comment 35** WD and LMA were the only traits where the correlation matched the predicted direction (*i.e.*, evidence that more drought-resistant traits are associated to taller trees), but ultimately neither of these traits were useful predictors of Rt . Furthermore, although correlations were statistically significant, trait variability within each height class overwhelmed any vertical trends (Fig. 2e-f).

Our findings support Hypothesis $H2.3$ that the observed tendency for larger trees to have greater growth reductions during drought (lower Rt) is driven by height itself, as opposed to more drought-sensitive traits in larger trees (Tables 1,5). As discussed above, there was little meaningful variation in traits with height at the community level. When $\ln[H]$ and hydraulic traits were considered together in multivariate models, the effect of $\ln[H]$ on Rt was consistently negative (Table 5). Simultaneously in the 1999 univariate model, this co-consideration resulted in a non-significant positive $\ln[H]$ - Rt correlation (Table 4).

Responses across droughts

Our results reject the hypothesis that overall community responses varied across droughts ($H3.1$). Within the context of mixed effects models, there were no significant differences in Rt across drought years (Table 4). **see comment 36**

Our findings give marginal support for Hypothesis $H3.2$, whereby we predicted directions of responses varied across droughts. In the majority of cases, response directions were consistent across droughts in both univariate and multivariate models (Tables 1,4,5). However, there were a few exceptions—most commonly in the categorical variables (CP and XP) but also for PLA_{dry} in one multivariate model for the 1999 drought (Tables 4, 5). These differences may be spurious as opposed to statistically meaningful. Among the univariate models, there was no instance where predictor variables significantly improved the models of two different droughts ($dAIC \geq 2$), but with contrasting coefficients (Table 4). Among the multivariate models, CP was not consistently in the top models for any drought (Table 5), and PLA_{dry} only appeared with a positive coefficient in the weakest predictor model of the six total models for the 1999 drought (contrasting with a negative coefficient in the univariate model; Table 4). It is probable that in the case of ring porosity, ring-porous species had lower Rt than diffuse- and semi-ring- porous species in the 1977 drought, contrasting with higher resistance in 1966 and 1999 (Tables 4,5). Note, however, that XP was not a significant predictor on its own for the 1977 drought.

Further, our findings support the hypothesis ($H3.3$) that the strength of predictor variables was different across the droughts (Tables 1,4,5). For instance, $\ln[H]$ and PLA_{dry} had much stronger negative effects in

1966 than in the other two years, $\ln[TWI]$ had the strongest negative effect in 1977, and XP (higher Rt among ring-porous trees) was strongest in 1999 (Tables 4,5). **see comment 37**

Discussion

Our results reveal how tree size, microenvironment, **see comment 38** and hydraulic traits shaped tree growth responses across three droughts in a temperate deciduous forest (Table 1). The greater susceptibility of larger trees to drought, similar to forests worldwide (Bennett et al., 2015), was driven primarily by their height (Liu and Muller, 1993; Stovall et al., 2019). There was a marginal additional effect of crown exposure, with the highest drought impacts felt by the most exposed and the most suppressed trees. This is consistent with observations of both the former (e.g., (Suarez et al., 2004); (Scharnweber et al., 2019)) and the latter (**REFS**). **see comment 39** There was no evidence that soil water availability increased drought resistance; in contrast, trees in wetter topographic positions experienced more growth reduction (consistent with (Zuleta et al., 2017; Stovall et al., 2019)), and larger rooting volume provided no advantage in the drier microenvironments. **see comment 40** The lower drought resistance of larger trees was not driven by a trend of more drought-sensitive species dominating the canopy. Drought sensitivity was also not consistently linked to species' LMA , WD , or xylem architecture. However, drought resistance was negatively correlated with the leaf hydraulic traits (PLA_{dry} , π_{tlp}) in the top overall model and the top models for two of the three individual droughts (Scoffoni et al., 2014; Bartlett et al., 2016; Medeiros et al., 2019). This is a novel finding in that PLA_{dry} and π_{tlp} have not previously been linked to drought growth responses. The direction of responses was mostly consistent across droughts, supporting the conclusion that they were driven by fundamental physiological mechanisms. However, the strengths of each predictor varied across droughts, indicating that specific drought characteristics interact with tree size, microenvironment, and traits to shape which individuals are most affected. These findings significantly advance our knowledge of the factors that confer vulnerability or resistance on trees during drought.

The droughts considered here were of similar severity (Fig. 1b) and fairly moderate **see comment 41**; droughts of this magnitude have occurred with an average frequency of approximately one per 10-15 years (Fig. 1a, Helcoski et al. (2019)). Therefore, we expect that most species are adapted, and individual trees acclimatized, to survive droughts of this nature when not coupled with other disturbances. **see comment 42,43** While the majority of trees experienced reduced growth, a substantial portion had increased growth (Fig. 1b), **see comment 44** supporting the observation that these droughts did not induce extreme stress on the entire forest. It is likely for this reason, along with other non-climate factors influencing tree growth, that our best models characterize only a modest amount of variation: 11-13% for all droughts combined, and 21-26% for each individual drought (Table 5). The moderate nature of these droughts is helpful for our analysis because it considers only trees that survived all of these droughts, and we lack information on the trees that were killed prior to 2008. These are likely to be relatively modest in number, and local forest monitoring data stretching back to the late 1980s confirms that the 1999 drought did not trigger major declines in tree abundance or biomass (*Anderson-Teixeira et al., in revision*). Thus, the droughts considered here are substantially weaker than others that have triggered massive tree die-off in other regions (e.g., (Allen et al., 2010)), many of which have shaped our understanding about the role of tree size (Bennett et al., 2015; Stovall et al., 2019) and-to some extent-traits underlying drought response mechanisms (Greenwood et al. (2017); Anderegg et al. (2016)). This is important because while our results are consistent with findings from more extreme, multiannual droughts, these extremes have not occurred in the Eastern United

States similar to the West, and therefore we do not know exactly how forests would respond under higher mortality conditions (Clark et al., 2016; Druckenbrod et al., 2019; Berdanier and Clark, 2016). Given this consistency with our results, however, we believe this is an indication of a more intensive response.

Our analysis indicates that height—as opposed to canopy position or soil water availability—is the primary factor through which tree size mediates drought response. Taller trees face inherent biophysical challenges in lifting water a greater distance against the effects of gravity and friction (Ryan et al., 2006; McDowell and Allen, 2015; McDowell et al., 2011; Couvreur et al., 2018). Vertical gradients in stem and leaf traits—including smaller and thicker leaves (higher LMA), more negative $P50$, and lower hydraulic conductivity at greater heights (Couvreur et al., 2018; Koike et al., 2001; McDowell et al., 2011)—make it biophysically possible for trees to become tall (Couvreur et al., 2018), yet height becomes a liability when drought incurs additional hydraulic challenges (Olson et al., 2018). Trade-offs can also occur, whereby traits conducive to efficient water transport may also lead to poor ability to recover from or re-route water around embolisms, for example in ponderosa pine (Roskilly et al., 2019). Taller trees also face different microenvironments (Fig. 2a-b), in part because they are more likely to be in dominant canopy positions (Fig. 2d). Even under non-drought conditions, evaporative demand increases with tree height while taller trees are more closely coupled to the atmosphere **see comment 45 (REFS- Jarvis 1984?; (Bretfeld et al., 2018; Kunert et al., 2017))**. Exposed canopy leaves reach higher temperatures (Smith and Nobel, 1977), particularly during drought when solar radiation tends to be higher and less water is available for evaporative cooling of the leaves. Correlation between height and canopy position (Fig. 2d) makes it challenging to disentangle the relative importance of height *per se* from microenvironment. However, significant decoupling between height and canopy position can be introduced by the configuration of neighboring trees (Fig. 2d) (Muller-Landau et al., 2006), and we show that height is a far stronger predictor of drought response than crown position for the three droughts evaluated in our study area (Tables 1,4,5).

Our analysis does have the limitation that canopy positions were re-cored in 2018 and undoubtedly changed for some trees since the 1960s, and we note that CP became an increasingly poor predictor moving back in time from 1999 to 1966 (Table 4). However, because trees would generally advance towards more dominant positions as they grow and as neighbors die, changing canopy positions would bias against the acceptance of $H1.2$. The implication is that dominant crown positions did have a marginally negative influence on Rt , which makes sense in light of the vertical environmental gradients described above and agrees with previous studies showing greater drought sensitivity in more exposed trees ((Suarez et al., 2004); (Scharnweber et al., 2019)). It is safe to assume that currently suppressed trees have always been suppressed, and their relatively low Rt (after correcting for height effects) is real, which is consistent with analyses showing that suppressed—and particularly crowded—trees can suffer disproportionately during drought (**REFS- Alan?**). **see comment 46** The observed height-sensitivity of Rt , together with the apparent lack of importance of soil water availability ($H1.3$), agrees with the concept that physiological limitations to transpiration under drought shift from soil water availability to the plant-atmosphere interface as forests age (Bretfeld et al., 2018), such that tall trees (dominant) are the most sensitive in mature forests. Additional research comparing drought responses of young and old forest stands, along with short and tall isolated trees, would be valuable for more clearly disentangling the roles of tree height and crown exposure.

The development of tree-ring chronologies for all dominant tree species at our site (Helcoski et al., 2019; Bourg et al., 2013) made it possible to compare historical drought responses across 12 species and their associated traits at a single site for the first time. At other sites, Elliot et al analyzed a number of species as

well, but responses were condensed into ring structure. Concerted measurement of leaf hydraulic traits of emerging importance (Scoffoni et al., 2014; Bartlett et al., 2016; Medeiros et al., 2019) allowed novel insights into the role of hydraulic traits in shaping drought response. The finding that PLA_{dry} and π_{tlp} can be useful for predicting drought responses—with both appearing in the top overall model and two of the three top models for each drought (Table 5)—is consistent with studies demonstrating that these are physiologically meaningful traits linked to species distribution along moisture gradients (Medeiros et al., 2019; Simeone et al., 2019; Maréchaux et al., 2015). Importantly, this finding indicates that both PLA_{dry} and π_{tlp} , which can be measured relatively easily (Bartlett et al., 2012; Scoffoni et al., 2014), hold promise for predicting drought growth responses across species. The importance of linking species’ traits to drought responses increases with tree species diversity; whereas it is feasible to study drought responses for all dominant species in most boreal and temperate forests (e.g., this study), this becomes difficult to impossible for species that don’t form annual rings, and for diverse tropical forests. Although progress is being made for the tropics (Schöngart et al., 2017), a full linkage hydraulic traits to drought responses would be invaluable for forecasting how little-known species and whole forests will respond to future droughts (REFS?—KAT/NOBBY/LAWREN).

see comment 48; the first paragraph was condensed here, but unsure where this should be put now Our analysis of hydraulic traits focused on species-level comparisons and did not characterize the role of variation with height. Further characterization of leaf hydraulic traits in relation to height and crown exposure would be valuable for enhancing our understanding of the interactive effects of tree height and traits on drought responses.

Although the physiological mechanisms discussed above lead to generally consistent directions of growth responses to tree height and hydraulic traits across droughts, indicating the universality of the underlying mechanisms, the relative importance of the drivers varied widely across droughts, indicating an interaction with drought characteristics (Tables 4-5). Although there were not significant differences in Rt among the drought years, Rt tended to be somewhat lower in 1966 (Fig. 1, Table 4). Height and dominant canopy position had stronger negative effects in this drought than in the others (Tables 4-5), which could potentially be linked to the key reality that this was the longest and most severe multiannual drought in recent history, increasing height’s propensity to be a stronger predictor of mortality (Stovall et al., 2019). **see comment 49** In 1977, which was the weakest drought in terms of PDSI (Fig. S2, Table S3), ring-porous species had lower Rt , contrasting with their higher Rt in the other two droughts and perhaps indicating that ring-porosity provides less of an advantage in terms of drought adaptation under less extreme droughts, consistent with Elliott et al. (2015). In the 1999 drought, which was the most intense in terms of growing season PDSI and the second-longest in duration, ring porosity was the most important predictor, with diffuse-porous species negatively impacted (Fig. S2). Thus, responses differed with the nature of each drought. Of course, site characteristics also define the nature of droughts, and comparisons of size and trait effects across sites—and across more droughts at a single site—would be of great value to elucidating the mechanisms through which drought characteristics interact with driver variables to shape tree growth responses.

As climate change drives increasing drought in many of the world’s forests (Trenberth et al., 2014; Intergovernmental Panel on Climate Change, 2015), the fate of forests and their climate feedbacks will be shaped by the biophysical and physiological drivers observed here. Large trees have been disproportionately impacted in forests around the world (Bennett et al., 2015; Stovall et al., 2019), and we show, at least at this site, that this is primarily driven by their height with some contributions from canopy position. The

distinction is important because it suggests that height *per se* makes trees vulnerable, even if their crowns are somewhat protected by neighbors, whereas solitary trees or the dominant trees in young regrowth forests should be less vulnerable. Considering just height and crown position, this would suggest that mature forests would be more vulnerable to drought than young, non-dense forests with short trees; however, soil water availability may limit the young forests (Bretfeld et al., 2018), and species traits often shift as forests age. Pioneer species at our site (*Liriodendron tulipifera*, *Quercus* spp., *Fraxinus americana*) **see comment 50** have a mix of traits conferring drought tolerance and resistance (Table 3), and further research on how hydraulic traits and drought vulnerability change over the course of succession would be valuable for addressing how drought tolerance changes as forests age (e.g. Rodríguez-Catón et al., 2015). In the meantime, the results of this study advance our knowledge of the factors conferring drought vulnerability and resistance in a mature forest, opening the door for more accurate forecasting of forest responses to future drought.

Acknowledgements see comment 51

Thanks to all researchers who helped to collect the data used here, in particular Jennifer C. McGarvey, Jonathan R. Thomson, and Victoria Meakem for original collection and processing of cores. Thanks also to Camila Medeiros for guidance on hydraulic and functional trait measurements, Edward Brzostek’s lab for collaboration on leaf sampling, and Maya Prestipino for data collection. This study was funded by the Smithsonian’s Forest Global Earth Observatory (ForestGEO), a Virginia Native Plant Society grant to KAT and AJT, and support from the Harvard Forest and National Science Foundation which supports the PalEON project (NSF EF-1241930) for NP.

Author Contribution

KAT, IM, and AT designed the research. Tree-ring chronologies were developed by RH under guidance of AT and NP. Trait data was collected by IM, JZ under guidance of NK and LS. Other plot data were collected by IM, AS, EGA, and NB under guidance of EGA and WM. Data analyses were performed by IM under guidance of KAT and VH. KAT and IM interpreted the results. IM and KAT wrote the first draft of manuscript, and all authors contributed to revisions.

References

- Abrams, M. D. (1990). Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology*, 7(1-2-3-4):227–238.
- Abrams, M. D. and Nowacki, G. J. (2016). An interdisciplinary approach to better assess global change impacts and drought vulnerability on forest dynamics. *Tree Physiology*, 36(4):421–427.
- Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., Troch, P. A., and Huxman, T. E. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*, 106(17):7063–7066.
- Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., Huxman, T. E., Hudson, P. J., Franz, T. E., Allen, C. D., Anderegg, L. D. L., Barron-Gafford, G. A., Beerling, D. J., Breshears, D. D., Brodribb, T. J., Bugmann, H., Cobb, R. C., Collins, A. D., Dickman,

- L. T., Duan, H., Ewers, B. E., Galiano, L., Galvez, D. A., Garcia-Forner, N., Gaylord, M. L., Germino, M. J., Gessler, A., Hacke, U. G., Hakamada, R., Hector, A., Jenkins, M. W., Kane, J. M., Kolb, T. E., Law, D. J., Lewis, J. D., Limousin, J.-M., Love, D. M., Macalady, A. K., Martínez-Vilalta, J., Mencuccini, M., Mitchell, P. J., Muss, J. D., O'Brien, M. J., O'Grady, A. P., Pangle, R. E., Pinkard, E. A., Piper, F. I., Plaut, J. A., Pockman, W. T., Quirk, J., Reinhardt, K., Ripullone, F., Ryan, M. G., Sala, A., Sevanto, S., Sperry, J. S., Vargas, R., Vennetier, M., Way, D. A., Xu, C., Yopez, E. A., and McDowell, N. G. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution*, 1(9):1285–1291.
- Allen, C. D., Breshears, D. D., and McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8):art129.
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., and Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4):660–684.
- Anderegg, W. R. L., Kane, J. M., and Anderegg, L. D. L. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3(1):30–36.
- Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., and Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, 113(18):5024–5029.
- Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K., Bowling, D. R., Gabbitas, R., Karp, D. S., Pacala, S., Sperry, J. S., Sulman, B. N., and Zenes, N. (2018). Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, 561(7724):538–541.
- Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Wright, S. J., Salim, K. A., Zambrano, A. M. A., Alonso, A., Baltzer, J. L., Basset, Y., Bourg, N. A., Broadbent, E. N., Brockelman, W. Y., Bunyavejchewin, S., Burslem, D. F. R. P., Butt, N., Cao, M., Cardenas, D., Chuyong, G. B., Clay, K., Cordell, S., Dattaraja, H. S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D. L., Ewango, C. E. N., Fischer, G. A., Fletcher, C., Foster, R. B., Giardina, C. P., Gilbert, G. S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W. W., Hart, T. B., Hau, B. C. H., He, F., Hoffman, F. M., Howe, R. W., Hubbell, S. P., Inman-Narahari, F. M., Jansen, P. A., Jiang, M., Johnson, D. J., Kanzaki, M., Kassim, A. R., Kenfack, D., Kibet, S., Kinnaird, M. F., Korte, L., Kral, K., Kumar, J., Larson, A. J., Li, Y., Li, X., Liu, S., Lum, S. K. Y., Lutz, J. A., Ma, K., Maddalena, D. M., Makana, J.-R., Malhi, Y., Marthens, T., Serudin, R. M., McMahon, S. M., McShea, W. J., Memiaghe, H. R., Mi, X., Mizuno, T., Morecroft, M., Myers, J. A., Novotny, V., Oliveira, A. A. d., Ong, P. S., Orwig, D. A., Ostertag, R., Ouden, J. d., Parker, G. G., Phillips, R. P., Sack, L., Sainge, M. N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H. S., Tan, S., Thomas, S. C., Thomas, D. W., Thompson, J., Turner, B. L., Uriarte, M., Valencia, R., Vallejo, M. I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., and Zimmerman, J. (2015a). CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology*, 21(2):528–549.

- Anderson-Teixeira, K. J., McGarvey, J. C., Muller-Landau, H. C., Park, J. Y., Gonzalez-Akre, E. B., Herrmann, V., Bennett, A. C., So, C. V., Bourg, N. A., Thompson, J. R., McMahon, S. M., and McShea, W. J. (2015b). Size-related scaling of tree form and function in a mixed-age forest. *Functional Ecology*, 29(12):1587–1602.
- Bartlett, M. K., Klein, T., Jansen, S., Choat, B., and Sack, L. (2016). The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. *Proceedings of the National Academy of Sciences*, 113(46):13098–13103.
- Bartlett, M. K., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K., and Sack, L. (2012). Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution*, 3(5):880–888.
- Bennett, A. C., McDowell, N. G., Allen, C. D., and Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1(10):15139.
- Berdanier, A. B. and Clark, J. S. (2016). Multiyear drought-induced morbidity preceding tree death in southeastern U.S. forests. *Ecological Applications*, 26(1):17–23.
- Beven, K. J. and Kirkby, M. J. (1979). A physically based, variable contributing area model of basin hydrology / Un modèle à base physique de zone d’appel variable de l’hydrologie du bassin versant. *Hydrological Sciences Bulletin*, 24(1):43–69.
- Bonan, G. B. (2008). Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science*, 320(5882):1444–1449.
- Bourg, N. A., McShea, W. J., Thompson, J. R., McGarvey, J. C., and Shen, X. (2013). Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large Forest Dynamics Plot. *Ecology*, 94(9):2111–2112.
- Bretfeld, M., Ewers, B. E., and Hall, J. S. (2018). Plant water use responses along secondary forest succession during the 2015–2016 El Niño drought in Panama. *New Phytologist*, 219(3):885–899.
- Bréda, N., Huc, R., Granier, A., and Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63(6):625–644.
- Clark, J. S., Iverson, L., Woodall, C. W., Allen, C. D., Bell, D. M., Bragg, D. C., D’Amato, A. W., Davis, F. W., Hersh, M. H., Ibanez, I., Jackson, S. T., Matthews, S., Pederson, N., Peters, M., Schwartz, M. W., Waring, K. M., and Zimmermann, N. E. (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*, 22(7):2329–2352.
- Condit, R. (1998). *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Condit, R., Watts, K., Bohlman, S. A., Pérez, R., Foster, R. B., and Hubbell, S. P. (2000). Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science*, 11(5):649–658.

- Cook, B. I., Ault, T. R., and Smerdon, J. E. (2015). Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*, 1(1):e1400082.
- Cook, B. I., Smerdon, J. E., Seager, R., and Coats, S. (2014). Global warming and 21st century drying. *Climate Dynamics*, 43(9):2607–2627.
- Couvreur, V., Ledder, G., Manzoni, S., Way, D. A., Muller, E. B., and Russo, S. E. (2018). Water transport through tall trees: A vertically explicit, analytical model of xylem hydraulic conductance in stems. *Plant, Cell & Environment*, 41(8):1821–1839.
- D’Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T., Houle, D., Arseneault, D., Beier, C. M., Bishop, D. A., Druckenbrod, D., Fraver, S., Girard, F., Halman, J., Hansen, C., Hart, J. L., Hartmann, H., Kaye, M., Leblanc, D., Manzoni, S., Ouimet, R., Rayback, S., Rollinson, C. R., and Phillips, R. P. (2018). Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. *Global Change Biology*, 24(6):2339–2351.
- Druckenbrod, D. L., Martin-Benito, D., Orwig, D. A., Pederson, N., Poulter, B., Renwick, K. M., and Shugart, H. H. (2019). Redefining temperate forest responses to climate and disturbance in the eastern United States: New insights at the mesoscale. *Global Ecology and Biogeography*, 28(5):557–575.
- Elliott, K. J., Miniati, C. F., Pederson, N., and Laseter, S. H. (2015). Forest tree growth response to hydroclimate variability in the southern Appalachians. *Global Change Biology*, 21(12):4627–4641.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N. (2006). Climate–Carbon Cycle Feedback Analysis: Results from the C4mip Model Intercomparison. *Journal of Climate*, 19(14):3337–3353.
- Friedrichs, D. A., Trouet, V., Büntgen, U., Frank, D. C., Esper, J., Neuwirth, B., and Löffler, J. (2009). Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees*, 23(4):729.
- Gonzalez-Akre, E., Meakem, V., Eng, C.-Y., Tepley, A. J., Bourg, N. A., McShea, W., Davies, S. J., and Anderson-Teixeira, K. (2016). Patterns of tree mortality in a temperate deciduous forest derived from a large forest dynamics plot. *Ecosphere*, 7(12):e01595.
- Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., Fensham, R., Laughlin, D. C., Kattge, J., Bönisch, G., Kraft, N. J. B., and Jump, A. S. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, 20(4):539–553.
- Guerfel, M., Baccouri, O., Boujnah, D., Chaïbi, W., and Zarrouk, M. (2009). Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Scientia Horticulturae*, 119(3):257–263.
- Hacket-Pain, A. J., Cavin, L., Friend, A. D., and Jump, A. S. (2016). Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. *European Journal of Forest Research*, 135(5):897–909.

- Harris, I., Jones, P. D., Osborn, T. J., and Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*, 34(3):623–642.
- Hartmann, H., Moura, C. F., Anderegg, W. R. L., Ruehr, N. K., Salmon, Y., Allen, C. D., Arndt, S. K., Breshears, D. D., Davi, H., Galbraith, D., Ruthrof, K. X., Wunder, J., Adams, H. D., Bloemen, J., Cailleret, M., Cobb, R., Gessler, A., Grams, T. E. E., Jansen, S., Kautz, M., Lloret, F., and O’Brien, M. (2018). Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytologist*, 218(1):15–28.
- Helcoski, R., Tepley, A. J., Pederson, N., McGarvey, J. C., Meakem, V., Herrmann, V., Thompson, J. R., and Anderson-Teixeira, K. J. (2019). Growing season moisture drives interannual variation in woody productivity of a temperate deciduous forest. *New Phytologist*, 0(0).
- Hoffmann, W. A., Marchin, R. M., Abit, P., and Lau, O. L. (2011). Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology*, 17(8):2731–2742.
- Intergovernmental Panel on Climate Change (2015). *Climate Change 2014: Impacts, Adaptation and Vulnerability: Working Group II Contribution to the IPCC Fifth Assessment Report. Volume 2 Volume 2*. OCLC: 900892773.
- Jennings, S. B., Brown, N. D., and Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry: An International Journal of Forest Research*, 72(1):59–74.
- Kannenberg, S. A., Novick, K. A., Alexander, M. R., Maxwell, J. T., Moore, D. J. P., Phillips, R. P., and Anderegg, W. R. L. (2019). Linking drought legacy effects across scales: From leaves to tree rings to ecosystems. *Global Change Biology*, 0(ja).
- Kennedy, D., Swenson, S., Oleson, K. W., Lawrence, D. M., Fisher, R., Costa, A. C. L. d., and Gentine, P. (2019). Implementing Plant Hydraulics in the Community Land Model, Version 5. *Journal of Advances in Modeling Earth Systems*, 11(2):485–513.
- Koike, T., Kitao, M., Maruyama, Y., Mori, S., and Lei, T. T. (2001). Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. *Tree Physiology*, 21(12-13):951–958.
- Kunert, N., Aparecido, L. M. T., Wolff, S., Higuchi, N., Santos, J. d., Araujo, A. C. d., and Trumbore, S. (2017). A revised hydrological model for the Central Amazon: The importance of emergent canopy trees in the forest water budget. *Agricultural and Forest Meteorology*, 239:47–57.
- Larjavaara, M. and Muller-Landau, H. C. (2013). Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. *Methods in Ecology and Evolution*, 4(9):793–801.
- Liu, H., Gleason, S. M., Hao, G., Hua, L., He, P., Goldstein, G., and Ye, Q. (2019). Hydraulic traits are coordinated with maximum plant height at the global scale. *Science Advances*, 5(2):eaav1332.
- Liu, Y. and Muller, R. N. (1993). Effect of Drought and Frost on Radial Growth of Overstory and Understory Stems in a Deciduous Forest. *The American Midland Naturalist*, 129(1):19–25.

- Lloret, F., Keeling, E. G., and Sala, A. (2011). Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12):1909–1920.
- Mankin, J. S., Seager, R., Smerdon, J. E., Cook, B. I., and Williams, A. P. (2019). Mid-latitude freshwater availability reduced by projected vegetation responses to climate change. *Nature Geoscience*, pages 1–6.
- Maréchaux, I., Bartlett, M. K., Sack, L., Baraloto, C., Engel, J., Joetzer, E., and Chave, J. (2015). Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest. *Functional Ecology*, 29(10):1268–1277.
- McDowell, N. G. and Allen, C. D. (2015). Darcy’s law predicts widespread forest mortality under climate warming. *Nature Climate Change*, 5(7):669–672.
- McDowell, N. G., Bond, B. J., Dickman, L. T., Ryan, M. G., and Whitehead, D. (2011). Relationships Between Tree Height and Carbon Isotope Discrimination. In Meinzer, F. C., Lachenbruch, B., and Dawson, T. E., editors, *Size- and Age-Related Changes in Tree Structure and Function*, Tree Physiology, pages 255–286. Springer Netherlands, Dordrecht.
- Meakem, V., Tepley, A. J., Gonzalez-Akre, E. B., Herrmann, V., Muller-Landau, H. C., Wright, S. J., Hubbell, S. P., Condit, R., and Anderson-Teixeira, K. J. (2018). Role of tree size in moist tropical forest carbon cycling and water deficit responses. *New Phytologist*, 219(3):947–958.
- Medeiros, C. D., Scoffoni, C., John, G. P., Bartlett, M. K., Inman-Narahari, F., Ostertag, R., Cordell, S., Giardina, C., and Sack, L. (2019). An extensive suite of functional traits distinguishes Hawaiian wet and dry forests and enables prediction of species vital rates. *Functional Ecology*, 33(4):712–734.
- Muller-Landau, H. C., Condit, R. S., Chave, J., Thomas, S. C., Bohlman, S. A., Bunyavejchewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K. E., Hart, T., Hubbell, S. P., Itoh, A., Kassim, A. R., LaFrankie, J. V., Lee, H. S., Losos, E., Makana, J.-R., Ohkubo, T., Sukumar, R., Sun, I.-F., Nur Supardi, M. N., Tan, S., Thompson, J., Valencia, R., Muñoz, G. V., Wills, C., Yamakura, T., Chuyong, G., Dattaraja, H. S., Esufali, S., Hall, P., Hernandez, C., Kenfack, D., Kiratiprayoon, S., Suresh, H. S., Thomas, D., Vallejo, M. I., and Ashton, P. (2006). Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters*, 9(5):575–588.
- NEON (2018). National Ecological Observatory Network. 2016, 2017, 2018. Data Products: DP1.00001.001, DP1.00098.001, DP1.00002.001. Provisional data downloaded from <http://data.neonscience.org/> in May 2019. Battelle, Boulder, CO, USA.
- Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., León-Gómez, C., Dawson, T., Martínez, J. J. C., Castorena, M., Echeverría, A., Espinosa, C. I., Fajardo, A., Gazol, A., Isnard, S., Lima, R. S., Marcati, C. R., and Méndez-Alonzo, R. (2018). Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences*, 115(29):7551–7556.
- Pretsch, H., Schütze, G., and Biber, P. (2018). Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *Forest Ecosystems*, 5(1):20.
- R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Rodríguez-Catón, M., Villalba, R., Srur, A. M., and Luckman, B. (2015). Long-term trends in radial growth associated with *Nothofagus pumilio* forest decline in Patagonia: Integrating local- into regional-scale patterns. *Forest Ecology and Management*, 339:44–56.
- Roskilley, B., Keeling, E., Hood, S., Giuggiola, A., and Sala, A. (2019). Conflicting functional effects of xylem pit structure relate to the growth-longevity trade-off in a conifer species. *PNAS*. doi: /10.1073/pnas.1900734116.
- Ryan, M. G., Phillips, N., and Bond, B. J. (2006). The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment*, 29(3):367–381.
- Scharnweber, T., Heinze, L., Cruz-García, R., van der Maaten-Theunissen, M., and Wilmking, M. (2019). Confessions of solitary oaks: We grow fast but we fear the drought. *Dendrochronologia*, 55:43–49.
- Schöngart, J., Bräuning, A., Barbosa, A. C. M. C., Lisi, C. S., and de Oliveira, J. M. (2017). Dendroecological Studies in the Neotropics: History, Status and Future Challenges. In Amoroso, M. M., Daniels, L. D., Baker, P. J., and Camarero, J. J., editors, *Dendroecology: Tree-Ring Analyses Applied to Ecological Studies*, Ecological Studies, pages 35–73. Springer International Publishing, Cham.
- Scoffoni, C., Vuong, C., Diep, S., Cochard, H., and Sack, L. (2014). Leaf Shrinkage with Dehydration: Coordination with Hydraulic Vulnerability and Drought Tolerance. *Plant Physiology*, 164(4):1772–1788.
- Simeone, C., Maneta, M. P., Holden, Z. A., Sapes, G., Sala, A., and Dobrowski, S. Z. (2019). Coupled ecohydrology and plant hydraulics modeling predicts ponderosa pine seedling mortality and lower treeline in the US Northern Rocky Mountains. *New Phytologist*, 221(4):1814–1830.
- Slette, I. J., Post, A. K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M. D., and Knapp, A. K. (2019). How ecologists define drought, and why we should do better. *Global Change Biology*, 0(0):1–8.
- Smith, W. K. and Nobel, P. S. (1977). Temperature and Water Relations for Sun and Shade Leaves of a Desert Broadleaf, *Hyptis emoryi*. *Journal of Experimental Botany*, 28(1):169–183.
- Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018a). Assessing terrestrial laser scanning for developing non-destructive biomass allometry. *Forest Ecology and Management*, 427:217–229.
- Stovall, A. E. L., Anderson-Teixeira, K. J., and Shugart, H. H. (2018b). Terrestrial LiDAR-derived non-destructive woody biomass estimates for 10 hardwood species in Virginia. *Data in Brief*, 19:1560–1569.
- Stovall, A. E. L., Shugart, H., and Yang, X. (2019). Tree height explains mortality risk during an intense drought. *Nature Communications*, 10(1):1–6.
- Suarez, M. L., Ghermandi, L., and Kitzberger, T. (2004). Factors predisposing episodic drought-induced tree mortality in *Nothofagus*— site, climatic sensitivity and growth trends. *Journal of Ecology*, 92(6):954–966.
- Sørensen, R., Zinko, U., and Seibert, J. (2006). On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth System Sciences*, 10(1):101–112.
- Trenberth, K. E., Dai, A., van der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., and Sheffield, J. (2014). Global warming and changes in drought. *Nature Climate Change*, 4(1):17–22.

- Twery, M. J. (1991). Effects of defoliation by gypsy moth. *IN: Gottschalk, Kurt W.; Twery, Mark J.; Smith, Shirley I., eds. Proceedings, U.S. Department of Agriculture interagency gypsy moth research review 1990; East Windsor, CT. Gen. Tech. Rep. NE-146. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 27-39.*, 146.
- Zhang, Y.-J., Meinzer, F. C., Hao, G.-Y., Scholz, F. G., Bucci, S. J., Takahashi, F. S. C., Villalobos-Vega, R., Giraldo, J. P., Cao, K.-F., Hoffmann, W. A., and Goldstein, G. (2009). Size-dependent mortality in a Neotropical savanna tree: the role of height-related adjustments in hydraulic architecture and carbon allocation. *Plant, Cell & Environment*, 32(10):1456–1466.
- Zuleta, D., Duque, A., Cardenas, D., Muller-Landau, H. C., and Davies, S. J. (2017). Drought-induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon. *Ecology*, 98(10):2538–2546.